

## **On the Monophyly of the Macrolepidoptera, Including a Reassessment of their Relationship to Cossioidea and Castnioidea, and a Reassignment of Mimallonidae to Pyraloidea**

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There have been persistent reports that the closest relatives of various Macrolepidoptera are the Cossioidea or Castnioidea. Thus Brock (1971) claimed that butterflies evolved from Castnioidea, Bombycoidea (including Sphingoidea) evolved from Cossioidea, and Noctuoidea-Geometroidea evolved from Pyraloidea. Brock's paper is a worthwhile contribution to certain aspects of morphology of adult Lepidoptera, but he failed to place exact character changes on the branches of his tree, so his tree cannot be considered either phylogenetic in any sense, or phenetic, but rather intuitive (of course, every author claims that his tree represents the one and only true phylogeny, but other workers have the right to demand proof in terms of actual characters).

However, a detailed examination of Lepidopteran anatomy of all life stages reveals that a very large number of characters separate the Cossioidea and Castnioidea from the Macrolepidoptera, and that the Macrolepidoptera form a monophyletic group. The traits are listed below and numbered, and the numbers placed on the phylogenetic tree (Fig. 1) where they changed in the manner described in the text. For larval traits, see Fracker, 1915; Petersen, 1965; Forbes, 1923-1960, and Common and Edwards, 1981. For pupae, see Mosher, 1916; Common, 1974.

No doubt there are dissenting views, and the author has no great personal experience with moth anatomy; others should publish their phylogenies, provided that they are supported by actual character changes and their exact positions on the lineage, so that objective judgments may be made about them.

### **Shared Derived Traits of Pyraloidea+Macrolepidoptera**

(1) On the larva, the postnatal ("subprimary") seta L3 was lost on the prothorax, leaving only L1 and L2. Nearly all other moths have L1, L2, and L3. (2) On the larva, only one L seta is on abdomen segment 9 (other moths have several). This trait is variable in Pyraloidea, in which some Pyralidae subfamilies have two L setae on A9, and Pterophoridae have many secondary setae, but Thyrididae, Carposinidae, Alucitidae, Mimal-

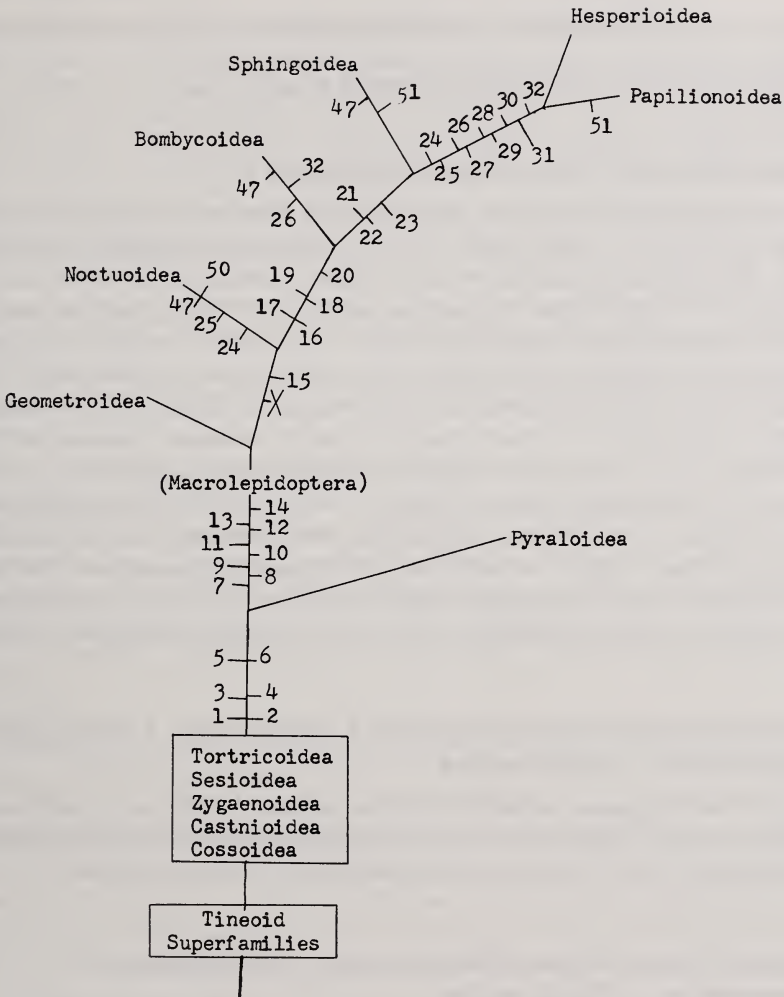


Fig. 1. Phylogeny of Ditrysian Lepidoptera. The numbers refer to gains, losses, or other alterations of the characters numbered and described in text (character 51 is in Table 1). X, possible origin of Bombycoidea-Sphingoidea, see text.

lonidae, and most Pyralidae subfamilies have only one L seta, indicating that one is the primitive state in the Pyraloidea. (3) On the pupal abdomen, only segments 5-6 (joints 4-5, 5-6, 6-7) are movable (in other Ditrysia, generally segments 3-7 move in males and 3-6 in females). (4) On the pupal abdomen, the segments lost their special spines and the pupa no longer protrudes from the larval burrow or cocoon (Tortricoidea, Sesioidea, Zygaenoidea, Castnioidea, and Cossoidea have two rows of backward-directed spines per abdomen segment used to wriggle out of the pupation site before adult emergence). The setose pupa of many Pterophoridae seems to be a later derivation; their long spines must have

another purpose entirely, as they lack a cocoon. (5) Wing vein M is vestigial in the discal cell (it is present, even branched, in most other moths). (6) Tympana evolved on the abdomen base.

### **Shared Derived Traits of Macrolepidoptera**

(7) On the larval abdomen, setae L1 and L2 became far apart; they are close together in other moths. (8) On the pupa, maxillary palpi were lost. (9) The adult maxillary palpi shrank to minute size (they are 3-4 segmented in Pyraloidea and earlier moths). (10) The jugal fold was lost on the forewing base (Sharplin, 1964). (11) The CuP wing vein became rudimentary, rather than a distinct functional vein in earlier moths. (12) Inside the adult mesothorax, the discrimen (of Ehrlich, 1958) became large (it is small in other moths, though moderate in size in Cossoidea). (13) In the adult thorax, the third metatergopleural muscle assumed an advanced state (Sharplin, 1964). (14) The postmedian wing lever (median wing process of Sharplin, 1964) became large (it is usually small in other moths). In addition, all Macrolepidoptera have the heart looped to the top of the thorax, which may be another shared derived trait, though some microlepidoptera also have a looped heart (Hessel, 1969).

### **Shared Derived Traits of Noctuoidea + Bombycoidea + Sphingoidea + Hesperioidea + Papilionoidea**

(15) The tympana moved to the metathorax. The lack of additional shared derived traits allows for the possibility that the Geometroidea is polyphyletic, but I will leave this possibility to other workers.

### **Shared Derived Traits of Bombycoidea + Sphingoidea + Hesperioidea + Papilionoidea**

(16) Secondary larval setae became abundant on older larvae. (17) The larval crochets diversified into two or three lengths (only one length in most other moths). (18) The two adult ocelli were lost. (19) On the adult mesothorax wall, the upper sector of the paracoxal sulcus ("precoxal suture" of Brock) was lost (Brock's "precoxal suture" in skippers actually is the secondary sternopleural sulcus). (20) The tympanum was lost.

### **Shared Derived Traits of Sphingoidea + Hesperioidea + Papilionoidea**

(21) The cocoon was lost. (22) The adult antennae are distally enlarged (antennae vary in more primitive moths, but filamentous antennae occur in nearly all groups). (23) On the adult mesothorax wall, the parepisternal rift was lost (Brock, 1971).

## Shared Derived Traits of Hesperioidea + Papilionoidea

(24) Eggs are upright. This is a rare condition, also possessed by Noctuoidea, and a few members within other moths (some Geometroidea, Choreutidae, Heliodinidae). Cossoidea and Castnioidea eggs have been stated to be upright, but actually both taxa have flat eggs (I. Common pers. comm.; Common and Edwards, 1981). (25) The larva has a ventral neck gland used for defense, as in Noctuoidea. (26) On the pupa, the foreleg femur is no longer visible as it is in nearly all moths. (27) The forewing lacks an areole, and vein  $R_{45}$  branches from R basad of  $R_1$  in the pupal wing (Zeuner, 1943). This areole occurs in most moths and in moths vein  $R_{45}$  branches distad of  $R_1$ . (28) On the adult mesothorax wall, the anapleural cleft is fused together and undetectable (Brock, 1971). (29) Inside the adult metathorax the furcal arms are mesally fused (Brock, 1971). (30) The adult heart is chambered where it loops to the top of the thorax (Hessel, 1969). The heart is looped in some moths, but only some Cossidae have a chambered heart (other Cossidae have only a ventral unchambered heart, indicating that the chamber of some Cossidae is just convergence). (31) On the adult abdomen, the anterodorsal apodemes on sternum 2 became minute (Brock, 1971). They are large in nearly all moths. (32) The adult wings lost the ability to be roofed over the abdomen.

I have not attempted to decipher the details of the phylogeny of the Ditrysians more primitive than Pyraloidea, except to determine that none of them are phylogenetically close to Macrolepidoptera. The most primitive Ditrysians, the Tineoid superfamilies, are distinguished from other Ditrysia by their (33) dual-rod coupling of abdomen sternum 2 with the thorax (Brock, 1971; Heppner, 1977). In addition, the Tineoid superfamilies (34) generally have only one row of backward-directed abdomen spines per segment (used to wriggle out of the cocoon or burrow), whereas Cossoidea, Castnioidea, Zygaenoidea, Sesiioidea, and Tortricoidea have two rows per segment (see character 4). The latter five superfamilies are rather similar. The Sesiioidea apparently branched from the Ditrysian trunk after the Cossoidea-Castnioidea-Zygaenoidea, after two wing base traits changed (Sharplin, 1964: (35) the metabasale lost its connection to the episternum or prescutum; (36) the insertion of the third metatergopleural muscle changed to an advanced condition). Tortricoidea apparently appeared still later after the Ditrysian trunk evolved (37) a true pointed and crocheted cremaster (present in Tortricoidea, Pyraloidea, and Macrolepidoptera), setting the stage for the appearance of Pyraloidea.

The persistent suggestions that various Macrolepidoptera evolved independently from various primitive Ditrysia (Brock, 1971, argued that butterflies evolved from Castnioidea, and Bombycoidea from Cossoidea) seem wrong on both cladistic and phenetic grounds, as detailed below.

Butterflies show numerous differences from Castnioidea and Cossoidea

(see in particular Common, 1974), including the previous characters 1, 2, 3, 4, 5, 7, 8 (see Common and Edwards, 1981), 9, 10 (see Common and Edwards, 1981), 11, 12, 13, 16 (secondary setae absent or rare in Cossioidea-Castnioidea), 17, 18, 19, 21, 22 (antenna somewhat clubbed but plumose-tipped in Castnioidea, simple to bipectinate in Cossioidea), 23, 24, 25, 27, 28, 29, 30, 31, 32, 35, 36, 37. In addition, the following traits differ between butterflies and Cossioidea-Castnioidea: (38) the larval crochets are in a circle or mesoserries in butterflies, in two transverse bands in Castnioidea and many Cossioidea; (39-40) the larval head is prognathous and strongly notched middorsally in Cossioidea-Castnioidea but not in butterflies; (41-43) the olfactory pits on the larval head are unusual in position in Cossioidea-Castnioidea (pit Pb is beside V1, La is far behind L1, Aa is near the P setae, Common and Edwards, 1981), normal in butterflies; (44) on the pupa, mandible remnants are definite bumps in Cossioidea-Castnioidea, but are weakly developed in butterflies (the "pilifers" of Mosher, 1916); (45) on the pupa a clypeolabral sulcus occurs in Cossioidea-Castnioidea but not in butterflies; (46) Cossioidea lack a proboscis, present in Castnioidea and butterflies; (47) chaetosema are absent in Cossioidea-Castnioidea, present in butterflies; (48) the mesepimeron on the adult thorax has a membranous division in most Cossioidea, lacking in Castnioidea and butterflies (Brock, 1971).

Obviously, these 41 traits demonstrate a vast gap separating Cossioidea-Castnioidea from butterflies. In fact, Cossioidea-Castnioidea are primitive members of the suborder Ditrysia, only slightly advanced from the Tineoidea. And the peculiar positions of the three olfactory pits (characters 41-43) on the larval head of Cossioidea-Castnioidea, (49) the lateral position of seta AF2 on the larval head (noted by Common and Edwards, 1981 and Hinton, 1946; my *Zygaenidae* larvae (first instar *Zygaena trifolii*) have these traits as well, except the position of pit Aa is normal), the absence of a proboscis, and the membranous epimeron cleft of Cossioidea surely indicate that the Cossioidea-Castnioidea-Zygaenoidea is a derived offshoot of the moth line which could not possibly have produced the butterflies or any other Macrolepidoptera. Evidently the superficial butterfly-like appearance, clubbed antennae, and day-flying habits of Castniidae have swayed the intuitive phylogenists, despite the vast morphological gap. Nevertheless, at least 16 families of moths have day-flying species with colorful wings, and the microscopic details of the antennae of Castniidae and Hesperiididae are very different (Jacqueline Miller, pers. comm.) despite their similar overall shape. Some Cossioidea have a chambered dorsal heart as in most butterflies (character 30), but other Cossids have the primitive ventral non-chambered heart (Hessel, 1969), so this must be convergence.

The story regarding the relationship between Sphingidae-Bombycoidea and Cossioidea-Castnioidea is much the same, though they are similar in these traits: the eggs of Bombycoidea are also flat (character 24), larvae

lack the neck gland (25), a cocoon is present (21), chaetosema are absent (47), antennae are bipectinate in Bombycoidea as in some Cossoidea (22), the anapleural cleft is a rift (28), a parepisternal rift occurs in Bombycoidea (23), the metafurcal arms are more similar (29), and the sternal apodemes are longer (31). But there still remain some 34 traits separating Sphingoidea from Cossoidea-Castnioidea, and 32 separating Bombycoidea from them. Evidently certain superficial similarities between Bombycoidea and Cossoidea (bipectinate antennae, loss of proboscis, and the presence of secondary setae in Limacodidae (including Megalopyginae) and Bombycoidea, similar adult appearance of Megalopyginae and Lasiocampidae) led intuitive phylogenists to claim a relationship, but obviously the relationship is not genealogical.

The relationship between Cossoidea-Castnioidea and Geometroidea-Noctuoidea shows the same wide gap, of course. In addition, Noctuoidea have: (50) a unique MD2 seta present on T3 and A1 (present in Notodontinae and other Noctuidae, Hinton, 1946); and Geometroidea-Noctuoidea have tympana (characters 6, 15). It seems probable that their tympana are descended from that of Pyralidae, because the Geometroid tympanum is on the first abdomen segment as in Pyralidae, and the Noctuid tympanum, which moved to the metathorax, retains a hood on the first abdomen segment and commonly has a ventral abdominal pouch that may have once possessed a tympanum. The Noctuid tympanum shows sufficient variation as to allow for the possibility that it is descended from the abdominal type.

The internal phylogeny of Macrolepidoptera seems straightforward except for the placement of Bombycoidea and Sphingoidea (see Table 1). The Geometroidea and Noctuoidea seem the most primitive Macrolepidoptera because their larvae generally lack secondary setae and retain one-length (uniordinal) crochets, their pupae retain the temporal cleavage line and the visible prothorax femur, their adults retain ocelli, tympana, and the upper sector of the paracoxal sulcus, and with Bombycoidea their adults retain the parepisternal rift and an areole. The Geometroidea with its flat eggs, abdominal tympana (as in Pyraloidea), and merely pectinate (not bipectinate) antenna is the more primitive of the two.

The most advanced group of Macrolepidoptera, butterflies, shares several derived traits with Noctuoidea: upright eggs, and a ventral larval neck gland used for chemical defense. While the latter gland may be convergent, or lost in other Macrolepidoptera, the upright eggs of butterflies-Noctuoidea are nearly unique (except in Heliodinidae, Choreutidae, and some Geometridae; the Cossidae, including Cossinae, and Castniidae always have flat eggs, I. Common, pers. comm. and Common and Edwards, 1981). If the upright egg is genuinely co-ancestral then the Bombycoidea-Sphingoidea branched off at point X of Figure 1. However, using the characters and weights of Table 1, the tree of Figure 1 is the most

Table 1. Characters of the Macrolepidoptera superfamilies. F, flat; U, upright; +, present; -, absent; M, mesoserries (medial crescent); O, oval; B, biordinal (two lengths); U, uniordinal; T, triordinal; S, simple or filamentous; P, pectinate (two projections from each antenna segment); B, bipectinate (four projections); C, clubbed. In addition, traits 28-31 are derived traits of butterflies (Hesperioidea-Papilionoidea), and 50 is a derived trait of Noctuoidea.

Trait	Geometroidea	Noctuoidea	Bombycoidea	Sphingoidea	Hesperioidea	Papilionoidea	Weight
16 secondary setae	- (+ prolegs)	- (+ rarely)	++	++	++	++	1
17 crochet length	B(U)	U(B)	B	B	T(B)	T(B)	½
18 ocelli	±	±	-	-	-	-	½
19 upper sector of paracoxal sulcus	±	±	-	-	-	-	½
20 tympana	±	±	-	-	-	-	½
21 cocoon	+	+	+	-	-	-	1
22 antenna shape	S,P	B,P,C,S	B,P (-)	C (P rare, short)	C	C	½
23 prepisternal rift	±	±	±	-	-	-	½
24 egg	F	U	F	F	U	U	1
25 ventral neck gland on larva	-	±	-	-	±	±	1
26 foreleg femur on pupa visible	±	±	-	±	-	-	½
27 areole	±	±	±	±	-	-	1
32 wings roofed over abdomen	±	±	-	±	-	-	½
38 crochet arrangement	M	M	M	M	O	M old O young	½
47 chaetosema	±	-	-	-	+	+	½
51 temporal cleavage line of pupa	±	±	±	-	+	-	1

parsimonious, requiring the fewest character changes of any of the possible trees. This is partly because the Bombycoidea-Sphingoidea-butterflies share certain traits (crochets always bi- or triordinal, secondary setae abundant, tympana and ocelli lost, and the upper sector of the paracoxal sulcus lost. Because three of these traits represent losses, there is some doubt about this parsimonious scheme, and first-instar butterflies have primary setae, whereas first-instar Bombycoidea-Sphingoidea apparently do not. Hopefully current and future research will add more characters to the table to resolve this question. At the present time Figure 1 seems most probable, which suggests that the ancestor of Bombycoidea-Sphingoidea-butterflies was a dayflier, resulting in the loss of tympana and ocelli, and the development of colorful wings. Sphingoidea and butterflies do share the loss of a cocoon and a roughly similar antenna.

Eye morphology may provide relevant characters within Macrolepidoptera (Horridge, 1975), and demonstrates similarities between skippers and other Macrolepidoptera. Many large nocturnal moths and skippers have a clear zone in the eye, and skippers are similar to Bombycoidea in having retinula cell extensions across the clear zone to the lens system (but skippers differ from Bombycoidea and others in lacking any anatomical wave guides) and skippers resemble Agaristidae in lacking pigment in the clear zone in daylight. Skippers and some night-adapted Macrolepidoptera have a well-focused eye, unlike Papilionoidea (one spot on the retina receives light focused from many ommatidia besides its own).

It should be noted that Mimallonidae (=Lacosomidae=Perophoridae), which have secondary setae only on the prolegs (Forbes, 1923, gives a setal map), have been placed in Bombycoidea and Geometroidea, but various traits place them in the Pyraloidea: abdominal setae L1 and L2 adjacent; sometimes two (or one) L setae on abdominal segment 9 (Fred Stehr, pers. comm.); only two postnatal prothorax L setae; crochets in a circle; a well-developed CuP vein.

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